

University of Groningen

Climb and flight speeds of shorebirds embarking on an intercontinental flight

Piersma, T.; Hedenstrom, A.; Bruggemann, J.H.; Hedenström, Anders

Published in:
Ibis

DOI:
[10.1111/j.1474-919X.1997.tb04628.x](https://doi.org/10.1111/j.1474-919X.1997.tb04628.x)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1997

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Piersma, T., Hedenstrom, A., Bruggemann, J. H., & Hedenström, A. (1997). Climb and flight speeds of shorebirds embarking on an intercontinental flight: Do they achieve the predicted optimal behaviour? *Ibis*, 139(2), 299-304. <https://doi.org/10.1111/j.1474-919X.1997.tb04628.x>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Climb and flight speeds of shorebirds embarking on an intercontinental flight; do they achieve the predicted optimal behaviour?

THEUNIS PIERSMA^{1,2}, ANDERS HEDENSTRÖM^{3,*} & J. HENRICH BRUGGEMANN⁴

¹ Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

² Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

³ Department of Ecology, Animal Ecology, Ecology Building, S-223 62 Lund, Sweden

⁴ Department of Marine Biology, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

Most Arctic-breeding waders wintering in West Africa cover the first 4000 km of their northward journey in spring by a single flight to western Europe. We examined the extent to which waders economize their flight behaviour during departure by comparing climb rates and forward flight speeds with predictions based on flight mechanic theory and the relevant morphological measurements made of birds collected on the site. With an optical range finder, we followed 98 wader flocks on their departure from Banc d'Arguin in Mauritania. We also measured wind speed and direction at different altitudes by tracking helium-filled balloons and thus were able to deduce airspeeds from groundspeeds of the departing flocks. Of the nine species examined, six showed the predicted negative relationship between climb rate and airspeed, although only one was statistically significant. By normalizing the data, we found a statistically significant negative correlation across all species. Although 17% of the observed climb rates were greater than the predicted theoretical maximum, the average observed climb rate was lower than the predicted optimum and the average observed airspeed was higher. The absolute deviations of climb rates from theory may have been because of the existence of pockets of rising and sinking air at the boundary of desert and ocean. That the absolute deviations in average climb rate and airspeed followed the predicted negative relationship is in accordance with the current theory of flight mechanics.

Avian migrants may be time or energy limited (Alerstam & Lindström 1990, Lindström & Alerstam 1992) and will be selected to make economic decisions about their flight behaviour (Alerstam & Lindström 1990). One aspect of optimization for consideration is the climb rate during departure on migratory flights in relation to expected wind conditions. Recently, a set of predictions concerning the selection of climb rate in departing migrants was presented by Hedenström and Alerstam (1992, 1994).

In the present paper, we describe the relationship between climb rate and forward flight speed in a sample of shorebird species of different body masses when embarking on a 3000–5000-km-long flight from West Africa to Europe (Zwarts *et al.* 1990). This flight is the first leg of their Afro–Arctic spring journey to the breeding grounds. Their tight time and energy budgets at this time of the year (Piersma 1987, Piersma & Jukema 1990) should have produced selection for economical flight performance. The aim of this study was to test the predicted negative relationship between climb rate and airspeed for a sample of species (Hedenström

& Alerstam 1992). We also present a test of the predictions by Hedenström and Alerstam (1994) on the optimal climb rate in relation to aerodynamic properties of the birds. This prediction is based on a simple minimization of the total energy cost for an entire migratory flight. It is then assumed that the birds will encounter a certain tailwind assistance at the cruising altitude. By exerting the maximum power available from the flight muscles while climbing (Hedenström & Alerstam 1992), there will be a trade-off between climb rate and forward airspeed. Thus, a high rate of climbing to cruising altitude will be associated with a relatively low forward airspeed and *vice versa*. The optimal policy is the climb rate that minimizes the total energy cost for the entire flight (Hedenström & Alerstam 1994). With expected strong wind assistance, it will generally pay to climb at a relatively fast rate.

Here we compare predicted climb rates with field observations obtained by an optical range finder (Piersma *et al.* 1990b). This data set is of particular relevance to test this optimization model since all species were migrating along the same flyway (Wymenga *et al.* 1990), along which probable wind conditions have been worked out from synoptic weather maps (Piersma & Van De Sant 1992).

* Corresponding author.

METHODS

Observations of departing shorebirds were made in the northwest corner of the Baie d'Aoutif (19°53'N, 16°17'W), which is part of a large area of intertidal flats, the Banc d'Arguin in Mauritania. The data in this paper were obtained between 21 April and 13 May during the 1988 spring migration season (for further details, see Piersma *et al.* 1990a). Departing flocks were identified and counted and notes on flight behaviour were made (see Piersma *et al.* 1990b for details). As many flocks as possible were tracked by an optical range finder (Barr and Stroud, Glasgow, Rangefinder No. 12 MK VII, Type FT37-No. 817; width between lenses 80 cm). The range finder gave distance, azimuth and elevation angles to the target.

The axis of the range finder was mounted perfectly vertically by the use of a water-levelling device. The protractor for the azimuth had a radius of 8 cm and could be read to the nearest 0.5°. We made sure that the smaller protractor indicating elevation (radius 3.5 cm, which could also be read to the nearest 0.5°) was indicating zero when the range finder was set to horizontal level by setting it at the horizon (which was easy to find in the flat desert landscape). Since the operator continuously adjusted the positions of the range finder's range meter to keep the two images of a disappearing flock superimposed, the accuracy of such readings should be determined by the accuracy of the range finder rather than by the person operating it. Fixes were read by a second observer within a 4-s interval. Polar coordinates of tracking observations were then transformed into Cartesian coordinates for analyses. Since it was obvious from the trackings over great distances that errors increased with increased distance (see Piersma *et al.* 1990b), we included only flocks up to 1000 m from the observer for *Calidris* species and the Turnstone *Arenaria interpres* and up to 2000 m for the larger species. Calibration measurements to fixed objects at known distances indicated that range finder measurements were accurate to within ± 10 m for a target at 500 m distance, ± 20 m at 1 km and ± 100 m at 2 km (Hedenström & Ålerstam 1994).

Wind speed and direction were measured by tracking helium-filled weather balloons with a theodolite (details in Piersma *et al.* 1990b). One observer tracked the disappearing balloon. Every 30 s, a second observer read the balloon's azimuth and elevation within 3 s, during which time the balloon had gained 90 m in height. These readings allowed the calculation of the changing locations of the balloon in three-dimensional space, the changes between projected horizontal coordinates at 30-s intervals, indicating wind speed and direction at successive 90-m height intervals. Balloons were followed up to 10,000 m; readings stopping at lower heights were because of low visibility (sand or dust storms). This method enabled us to determine the airspeed of the flying birds by taking into account the wind vector at the altitude where the flocks were flying.

For calculations of predicted optimal flight performance, information on lean body mass (LBM), fuel load and wing-

span are required. A summary of these data and sources is given in Table 1.

Calculation of maximum sustainable power output from the flight muscles (P_{\max}) requires an estimate of muscle mass and wing-beat frequency. Muscle masses were obtained from carcass analyses of samples of birds collected on the Banc d'Arguin (Piersma & Van Brederode 1990; Table 1). We used Pennycuick's (1994) formula to calculate wing-beat frequency. Video films of climbing Knots *Calidris canutus* in Iceland (Hedenström & Ålerstam 1990) gave 9% higher wing-beat frequency than Pennycuick's formula. Hence, to adjust for climbing flight, we added 9% to the values calculated by the formula. Power available was then calculated as wing-beat frequency multiplied by muscle work. We used a value of 21.2 J per kg for mass-specific muscle work (Pennycuick & Rezende 1984).

Flight mechanical calculations of power and characteristic flight speed follow Pennycuick (1975, 1989). Calculations of maximum and optimal climb rates follow Hedenström and Ålerstam (1992, 1994).

RESULTS

The data for all species showed a large scatter, with a tendency towards a negative relationship between airspeed and climb rate (Fig. 1). However, for only one species, the Grey Plover *Pluvialis squatarola*, was the negative correlation significant. Therefore, we normalized the data by dividing observed airspeed by the predicted minimum power speed V_{mp} (Pennycuick 1975, 1989; Table 1) and divided observed climb rate by the calculated maximum climb rate $V_{z,max}$ (Hedenström & Ålerstam 1992; Table 1). This gave us a single data set which showed a significant overall negative correlation across all species ($r_{96} = -0.30$, $P < 0.01$). An analysis of covariance showed a significant effect of species identity ($r^2 = 0.31$, $F_{9,7.7} = 6.39$, $P < 0.001$) and normalized airspeed ($r^2 = 0.10$, $F_{9,7.1} = 14.2$, $P < 0.001$) but not of flock size ($F_{9,7.1} = 2.20$, n.s.) on the normalized rate of climb. The scattergram of the normalized data is shown in Figure 2, together with the theoretical envelope of climb rate v airspeed. The envelope defines the relationship between theoretical climb rate and airspeed, where horizontal and vertical axes at 1 represent $V_{z,max}$ and V_{mp} , respectively. Figure 2 shows that very few observed airspeeds were below V_{mp} , while as many as 17% of the observations with airspeed above V_{mp} showed an associated climb rate higher than predicted by $V_{z,max}$.

Predicted optimal climb rate and the associated airspeed as well as observed climb rate and airspeed of the departing shorebirds are shown in Table 2. The predicted value of optimal climb rate was calculated on the basis of an expected wind assistance of 4 m per s, as evaluated by Piersma and Van De Sant (1992) for this flyway. Generally, the observed airspeeds were higher than predicted while the observed climb rates were lower than predicted. All except one of the observed climb rates differed significantly from the

Table 1. Morphological data and wing-beat frequency for the wader species observed departing in climbing flight from Banc d'Arguin, Mauritania

Species	m_0^a (kg)	h^b	Muscle frac- tion (% m_0)	b^c (m)	AR	f^d (Hz)	V_{mp} (m/s)	$V_{z,max}$ (m/s)
Dunlin <i>Calidris alpina</i>	0.039	1.59	20	0.34	8.0	11.5	6.5	1.66
Sanderling <i>Calidris alba</i>	0.043	1.51	20	0.38	8.7	10.2	6.3	1.64
Turnstone <i>Arenaria interpres</i>	0.095	1.41	24	0.47	8.4	9.3	7.2	1.92
Redshank <i>Tringa totanus</i>	0.109	1.36	23	0.62	8.9	6.4	6.5	1.29
Knot <i>Calidris canutus</i>	0.119	1.33	20	0.51	9.1	8.9	7.4	1.42
Greenshank <i>Tringa nebularia</i>	0.174	1.49	25	0.69	9.9	6.8	7.4	1.16
Grey Plover <i>Pluvialis squatarola</i>	0.191	1.32	22	0.60	10.6	8.4	8.0	1.46
Bar-tailed Godwit <i>Limosa lapponica</i>	0.238	1.39	21	0.68	9.2	7.4	8.3	0.87
Whimbrel <i>Numenius phaeopus</i>	0.425	1.32	18	0.82	6.7	6.1	9.2	1.77

Abbreviations: m_0 = fat-free body mass; h = fuel factor (body mass at departure divided by m_0); b = wingspan; AR = aspect ratio (wingspan squared divided by wing area); f = estimated wing-beat frequency; V_{mp} = calculated minimum power speed; $V_{z,max}$ = calculated maximum climb rate.

^a From body composition analysis of collected specimens at Banc d'Arguin (Piersma & Van Brederode 1990); Greenshank autumn mass in South Africa (Cramp & Simmons 1983).

^b Fuel fractions calculated from departure masses given by Zwarts *et al.* (1990); Greenshank spring mass in South Africa (Cramp & Simmons 1983).

^c Our own unpublished data and Cramp & Simmons (1983).

^d Pennycuick (1990) adjusted for climbing flight.

predicted value, but for Whimbrel *Numenius phaeopus*, the observed climb rate was higher than predicted (Table 2). Airspeeds were consistently higher than predicted and significantly so in five of the nine cases (Table 2).

DISCUSSION

The outcome of the present study is that the predicted negative relationship between climb rate and airspeed was corroborated, while the observed climb rates tended to be lower and the associated forward airspeeds higher than predicted by Hedenström and Ålerstam (1994) for an expected wind assistance of 4 m per s (Piersma & Van De Sant 1992). Hedenström and Ålerstam (1994) presented data on the climb rates in two shorebird species departing from Iceland on spring migration which were not significantly different from the predicted values. When there is no expected wind assistance the model predicts maximum range airspeed during the climb phase, but also this situation underestimated forward speed and overestimated climb rate as compared with the field observations. If the birds are time minimizers (Ålerstam & Lindström 1990), then the optimal flight speed is higher than maximum range speed. The difference is rather small and we do not think that optimal forward airspeed associated with time-minimization migration can account for the relatively low climb rates observed.

The relationship between climb rate and airspeed was rather weak, and the variation of the climb rate data was

substantial (coeff. var. = 79.4% for the normalized data), while airspeed did not vary to the same extent (coeff. var. = 24.6%). In fact, 17% of the observations fell above the calculated theoretical maximum. Both the theoretical predictions and the field measurements may be biased. Some potential sources of error and their possible influence on theoretical predictions and field measurements will be discussed briefly.

The aerodynamic theory used for the calculation of optimal climb rates involves certain assumptions about aerodynamic properties of the birds (Pennycuick 1989). Recently, Tucker (1990) showed that the body drag coefficient may be lower than the range used in Pennycuick's theory. A lower body drag coefficient would lead to higher predicted optimal climb rates, and the discrepancy between predictions and observations would increase.

Potential errors in the carcass analyses are unlikely since the relative muscle masses are within a few percent of those obtained in other studies (cf. Marden 1987).

The value used for mass-specific muscle work of shorebirds (Pennycuick & Rezende 1984) may be somewhat higher than the value used in the predictions, 21.2 J per kg (Hedenström & Ålerstam 1992:table 3). Increasing this parameter also leads to higher predicted optimal climb rates and thus would take the predictions further away from the field observations. Recently, Ellington (1991) evaluated existing methods used to estimate the power available from the flight muscles. By using data on maximum load lifting capacity (Marden 1987), Ellington arrived at a mean value

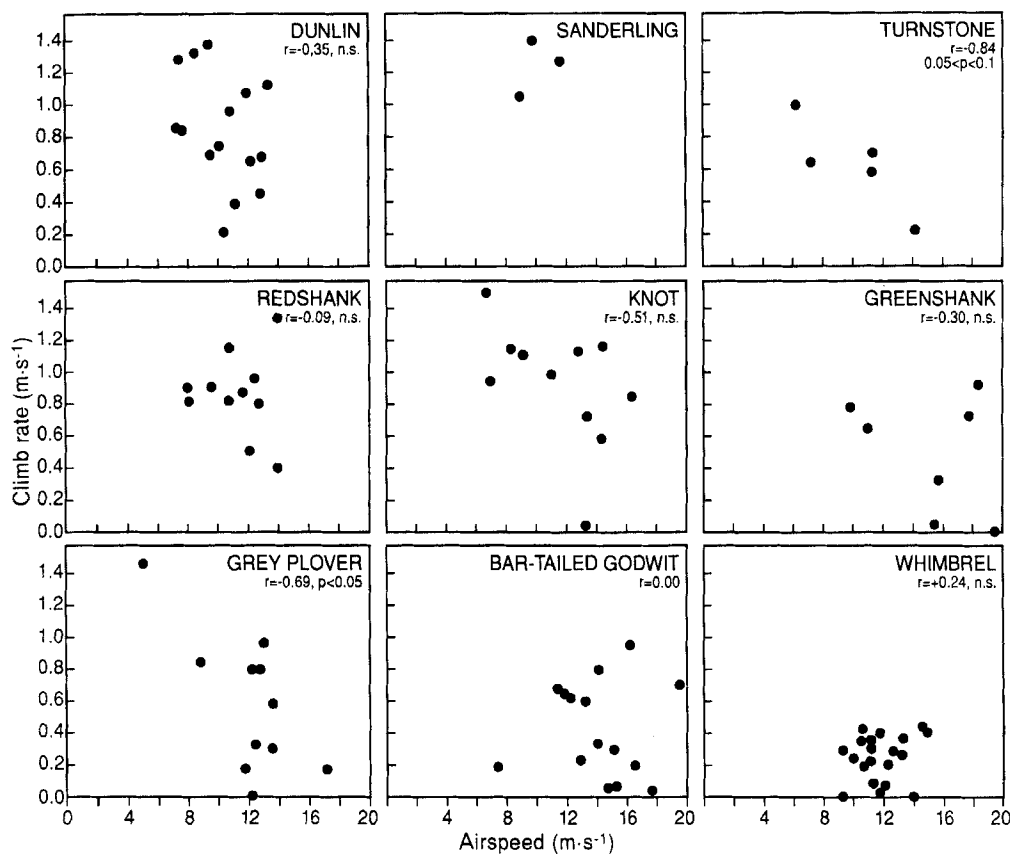


Figure 1. Correlations between climb rate and airspeed of flocks of different species of waders departing from the Baie d'Aouatif, Banc d'Arguin, Mauritania, April–May 1988.

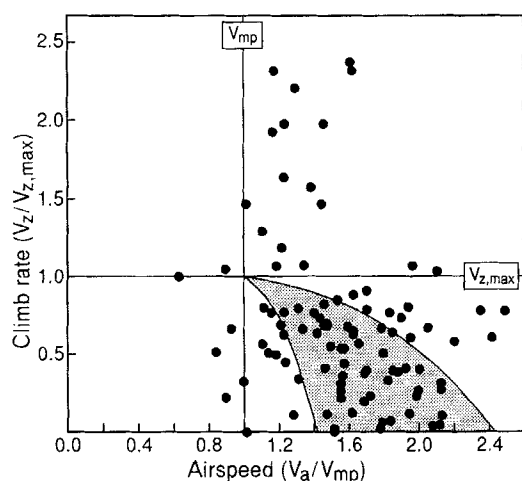


Figure 2. Climb rate as a function of airspeed on the basis of normalized data for all departing flocks of waders presented in Figure 1. Climb rate of each flock has been divided by the theoretically maximum climb rate for that species and airspeed has been divided by the relevant minimum power speed. The shaded envelope encloses the theoretical relationships between climb rate and airspeed (Hedenström & Ålerstam 1994) for all included species.

for muscle mass-specific power output of 171 W per kg for birds. Applying this value to our calculations of P_{\max} and recalculating the predicted airspeeds and climb rates changed the outcome of the comparison between prediction and field observation in a few cases. Thus, the observed climb rates in Dunlin *Calidris alpina* and Knot were not significantly different from the predictions, and the observed airspeed of the Whimbrel was not significantly different from the prediction. However, the trend of on average lower observed climb rates than those predicted mostly remained after adjusting the estimated P_{\max} .

Theoretically, flying in flock formation can save birds energy (Lissaman & Shollenberger 1970, Hummel 1983), which can be used for increasing either airspeed or climb rate. In one study, shorebirds were reported to increase speed with increased flock size in horizontal flight (Noer 1979). We found no significant influence of flock size on climb rate nor on airspeed.

The great scatter in the data set, with some observations even falling above the theoretical maximum, warrants some caution. It could be that some flocks experienced external lift and therefore showed higher climb rates than the possible maximum, which refers to climb rate relative to the surrounding air. However, most of the trackings referred to

Table 2. Observed airspeeds and climb rates for the wader species departing from the Bank D'Arguin, Mauritania. Predicted values are based on the assumption of an expected tailwind of 4 m per s (all values are in m/s)

Species	V_a	$V_{a,obs}$	s.d.	n	V_c	$V_{c,obs}$	s.d.
Dunlin <i>Calidris alpina</i>	8.7	10.5**	2.05	15	1.55	0.84***	0.35
Sanderling <i>Calidris alba</i>	8.4	10.1 n.s.	1.34	3	1.55	1.24 n.s.	0.18
Turnstone <i>Arenaria interpres</i>	9.8	10.0 n.s.	3.28	5	1.80	0.63***	0.27
Redshank <i>Tringa totanus</i>	8.8	11.2**	2.08	11	1.21	0.85***	0.26
Knot <i>Calidris canutus</i>	9.9	11.4 n.s.	3.28	11	1.31	0.92**	0.38
Greenshank <i>Tringa nebularia</i>	9.9	15.5**	3.66	7	1.07	0.49**	0.36
Grey Plover <i>Pluvialis squatarola</i>	10.8	12.1 n.s.	3.00	11	1.34	0.58***	0.43
Bar-tailed Godwit <i>Limosa lapponica</i>	10.7	14.1***	2.86	15	0.78	0.42***	0.29
Whimbrel <i>Numenius phaeopus</i>	10.2	11.9***	1.58	20	0.17	0.24*	0.14

Abbreviations: V_a , V_c = predicted airspeed and climb rate, respectively; $V_{a,obs}$ and $V_{c,obs}$ = mean observed airspeed and climb rate; s.d. = standard deviation for sample; n = sample size.

Significance of sample mean from predicted value: n.s. = $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

flight over a narrow peninsula close to tidal flats and the sea (Piersma *et al.* 1990:fig. 8). Usually, convective thermals develop over land (Bradbury 1989). If the flat sandy desert east of the Baie d'Aouatif fuels the development of thermals, there should be an associated sink over the tidal flats, peninsula and sea at the western rim. Hence, without having measured vertical winds, it is possible that the majority of the flocks were flying through sinking air, and hence our measurements underestimated the real climb rates. If the birds experienced that they were flying through a sink, the relatively high forward speeds, which were higher than the predictions, can also be explained by the influence of downward vertical winds (Nisbet 1962, Pennycuik 1969).

Wader flocks departing on a 4000–5000-km-long migration flight from Mauritania to staging areas in Europe showed a negative correlation between climb rate and airspeed. Climb rates in most of the species were on average lower than predicted by the optimization model of Hedenström and Ålerstam (1994). However, since the associated forward airspeeds were higher than predicted, the deviations followed the theoretical relation between climb rate and airspeed and could be the result of an unmapped mosaic of rising and sinking air in this coastal zone exploited by the departing migrants.

We thank Luit Buurma and Hans Reiff for suggesting the methodology and for making available the instruments; HoekLoos BV for gratis helium; Yaa Ntiama-Baidu and Abou Gueye for help in the field; Tom van Spanje, Wim Wolff and the Foundation for International Wader and Waterfowl Research (WIWO) for organizational arrangements; Thomas Ålerstam, Susanne Åkesson and Torbjörn Fagerström for encouragement, comments and suggestions and Dick Visser for drawing the figures. Financial support for the field work was obtained from Bachiene Foundation, British Ornithologists' Union, Commission of the European Communities, Fund for Research for Nature Conservation (FONA), Netherlands' Ministry of Agriculture and Fisheries, National Geographic Society, Natuurmonumenten, Prince Bernhard Fund, Shell Internationale Research

Maatschappij, Netherlands' State Forestry Service (Staatsbosbeheer) and Research Institute for Nature Management.

REFERENCES

- Ålerstam, T. & Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. In E. Gwinner (ed.) *Bird Migration*: 331–351. Berlin: Springer-Verlag.
- Bradbury, T. 1989. *Meteorology and Flight: A pilot's guide to weather*. London: A&C Black.
- Ellington, C.P. 1991. Limitations on animal flight performance. *J. Exp. Biol.* 160: 71–91.
- Hedenström, Å. & Ålerstam, T. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* 164: 19–38.
- Hedenström, Å. & Ålerstam, T. 1994. Optimal climbing flight in migrating birds: Predictions and observations of Knot and Turnstone. *Anim. Behav.* 48: 47–54.
- Hummel, D. 1983. Aerodynamic aspects of formation flight in birds. *J. Theor. Biol.* 104: 321–347.
- Lindström, Å. & Ålerstam, T. 1992. Optimal fat loads in migrating birds: A test of the time-minimization hypothesis. *Am. Nat.* 140: 477–491.
- Lissaman, P.B. & Shollenberger, C.A. 1970. Formation flight of birds. *Science* 168: 1003–1005.
- Marden, J.H. 1987. Maximum lift production during take off in flying animals. *J. Exp. Biol.* 130: 235–258.
- Nisbet, I.C.T. 1962. Thermal convection and trans-Saharan migration. *Ibis* 104: 431.
- Noer, H. 1979. Speeds of migrating waders Charadriidae. *Dansk Orn. Foren. Tidsskr.* 73: 215–224.
- Pennycuik, C.J. 1969. The mechanics of bird migration. *Ibis* 111: 525–556.
- Pennycuik, C.J. 1975. Mechanics of flight. In Farner, D.S. & King, J.R. (eds) *Avian Biology*, Vol. 5: 1–75. New York: Academic Press.
- Pennycuik, C.J. 1989. *Bird Flight Performance. A practical calculation manual*. Oxford: Oxford University Press.
- Pennycuik, C.J. 1990. Predicting wingbeat frequency and wavelength of birds. *J. Exp. Biol.* 150: 171–185.

- Pennycuik, C.J. & Rezende, M.A. 1984. The specific power output of aerobic muscle, related to the power density of mitochondria. *J. Exp. Biol.* 108: 377–392.
- Piersma, T. 1987. Hop, skip or jump? Constraints on migration of Arctic waders by feeding, fattening and flight speed. *Limosa* 60: 185–191 [in Dutch with English summary].
- Piersma, T. & Jukema, J. 1990. Budgeting the flight of a long-distance migrant: Changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* 78: 315–337.
- Piersma, T. & Van Brederode, N.E. 1990. The estimation of fat reserves in coastal waders before their departure from northwest Africa in spring. *Ardea* 78: 221–236.
- Piersma, T. & Van De Sant, S. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica* 2: 55–66.
- Piersma, T., Zwarts, L. & Bruggemann, J.H. 1990a. Behavioural aspects of the departure of waders before long-distance flights: Flocking, vocalizations, flight paths and diurnal timing. *Ardea* 78: 157–184.
- Piersma, T., Klaassen, M., Bruggemann, J.H., Blomert, A.-M., Gueye, A., Ntiama-Baidu, Y. & Van Brederode, N.E. 1990b. Seasonal timing of the spring departure of waders from the Banc d'Arguin, Mauritania. *Ardea* 78: 123–134.
- Tucker, V.A. 1990. Body drag, feather drag and interference drag of the mounting strut in a Peregrine Falcon, *Falco peregrinus*. *J. Exp. Biol.* 149: 449–468.
- Wymenga, E., Engelmoer, M., Smit, C.J. & Van Spanje, T.M. 1990. Geographical breeding origin and migration of waders wintering in West Africa. *Ardea* 78: 83–112.
- Zwarts, L., Ens, B.J., Kersten, M. & Piersma, T. 1990. Molt, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* 78: 339–364.

Submitted 29 November 1995; revision accepted 7 April 1996